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The Still under Construction Cercopithecinae Phylogeny

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Several genera of haplorhines characterize the biodiversity of the tropical/equatorial belt of Africa, with a high rate of sympatry. Phylogenetic relationship of the taxa, in spite of time, aim and general efforts, are still ineffectually known. The relative young age of fossils related to these genera suggests a Plio-Pleistocene differentiation in sub-Saharan Africa.

Within these taxa, subfamily Cercopithecinae (guenons and related monkeys) demonstrates several characters of uniqueness and high rates of sympatry that still need a comprehensive and deep evaluation in order to understand the origin and the phylogeny of the group.

Actually they show the most intense coat patterns differentiation and the widest variability in chromosome number and in syntenic organisation.

From the Systematic point of view Cercopithecinae are a diversified group of primates that includes the genera *Cercopithecus, Chlorocebus, Allenopithecus, Miopithecus* and *Erythrocebus.* Recently the *C. l'hoesti* group has been classified in the genus *Allochrocebus*. This grouping composes the Cercopithecini tribe with about 36 species.

All these monkeys have an undifferentiated skeleton morphology and light body structure adapted to an efficacious deep-forest arboreal life. Tropical forests should have been the environment of the ancestor of the group as nowadays shows a large distribution in African forests (i.e. in present relict forested areas), from Senegal to Uganda, from Eastern Congo to Angola.

Proposed exceptions to this evolutionary hypothesis regard, first and foremost, two (sister) genera: *Allenopithecus* (sp. *nigroviridis*) (Allen's Swamp monkey), and the *Erythrocebus* (sp. *patas*) (Patas monkey, Hussar monkey).

Allenopithecus has been generally considered a representative of an ancestral stock of forestal cercopithecini [1]; it is distributed in swampy areas in the Zaire basin, and frequently reported ranging at ground level. *Erythrocebus* is distributed in the semiarid belt that characterises African sub-Saharan regions, from Senegal all the way east to the South Sudan and south way to Tanganika's savannas. Particularly adapted to its ecology it is an efficacious ground-dweller and runner.

From a systematic point of view, Allen's monkey and Patas monkey have very different characters but their condition of terrestriality persuaded several authors to suggest, since the '80s, a possible grouping in a separate clade of ground-dwellers, with ancestral peculiarities. These evaluations, and other data added to the discussion, coming from chromosomal analysis [2,3] and from different molecular approaches [4,5] reiterated the proposal of a subdivision of the subfamily in two main clades of terrestrial (ancestral) and strictly arboreal monkeys. Furthermore other taxa have been intermittently involved in the condition of ancestral representative of the subfamily. The Dwarf monkey *Miopithecus* (sp- *talapoin*) [6,7] strictly arboreal; the largely dispersed savannas green-monkey *Chlorocebus (Cercopithecus) aethiops,* and the *Cercopithecus (Allochrocebus) l'hoesti* [8] that the authors consider as terrestrial but, according to the tradition, and to my experience, is a low strata montane forest tree-dweller. The availability of a more representative set of species allowed Paulina Perelman [9] to produce a new molecular phylogeny of the tribe. This proposal includes a reversed interpretation, in respect to the critical features of terrestriality and ancestrality. Further, according to this study, the tribe underwent a recent speciation with an "early offshoot" from an ancestral notch (dated near 7 mya), of *Miopithecus* (arboreal) and *Allenopithecus* (trendily terrestrial) in respect to Guenons (*Cercopithecus* spp). The authors conclude saying that a revision of the cercopithecini systematics is urgent. And this is absolutely true.

The situation is evidently confused and the different phylogenetic interpretation, as derived from different experimental approaches appears, from the zoological point of view, very heterogeneous, and definitively vague.

Few considerations are necessary in order to understand the need for this academic discussion. The guenons of the genus *Cercopithecus* appear morphologically uniform and have a wide and overlapping biogeography in western and central forests. This overlapping gave several cues to the depiction of polyspecific associations (even with mangabey) and hybridization (since the historical descriptions of Aldridge-Blake and Struhsaker). Presumably this complicate biogeography has driven their intriguing facial and genital colour patterning, their intense vocal communication and their genetics and reproductive biology. If we start from the hypothesis of a group presumably arisen via adaptation from a ground-dweller common ancestor, we must find, at least in one cluster, hands and feet that clearly demonstrate this stable ecological choice: appendicular bones that are expressive of a ground living specialisation. In a group of terrestrial primates that moves on digits, like Papionini (the other tribe in the Subfamily, with different evolutionary histories inside), we find a huge calcaneum and a semi-vertical shape of the calcaneo-cuboid facet. When we consider [10] hands and feet anatomy of the over mentioned species in Cercopithecinae we find that *Allenopithecus* has a cercopithecus-like hand, the foot demonstrates a rate of efficaciousness to terrestriality, but the calcaneum indicates that the animal has a basic arboreal specialization. *Chlorocebus (Cercopithecus) aethiops* has admixed characters towards a more cursorial locomotion, with the calcaneum that clearly indicates an aptitude to climbing, suggesting that cursorial features are secondarily acquired. *C. (A.) l'hoesti* is a mosaic analogous to the green-monkey: derived traits are superimposed on a predominantly arboreal body composition. Only *E. patas* shows an extreme adaptation to a sprinter gait, starting from its body composition that is slender and sinuous, with long appendicular skeleton, short digits and elongated calcaneum and metatarsals.

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These evidences do not support a phylogenetically significant separation of neither the tribe nor a terrestrial ancestor, but indicate only a tendency, for some genera, to a secondarily acquired attitude to ground-dwelling, evidently related to ecological pressures. However, these taxa maintain features of a tree-dwelling specialisation. Furthermore, multidisciplinary approaches to the interpretation of cranial morphology in cercopithecini indicate a lack of cluster inside the tribe [11]. These data follow the early evaluations of Martin and McLarnon [12] on skull ergonomy and teeth morphology that, in effect, did not support neither the separation of African guenons in two subgroups, nor the ancestral position of *A. nigroviridis* in respect to sympatric (and allopatric) guenons.

Even the chromosomal evidences of tribe clustering are not convincing. It is well known that Cercopithecinae diploid number is highly variable (2n ranges from 46 to 72) [13]. Their vivacious genomic organization has been considered an extraordinary gymnasium for the understanding of chromosomal dynamics in genomic evolution and speciation. Early chromosome evolution studies proposed, in the light of chromosomal fission-fusion theory, a tendency, inside the phylogeny, to the increase of diploid number (and complexity) in time, and a basal position of low diploid numbers kayotypes (*Allenopithecus* 2n=48, with a karyotype organisation analogous to Papionini). This approach strongly supported the clusterization of the tribe in two groups: trendily terrestrial and chromosomally conservative monkeys, and arboreal and chromosomally not conservative guenons. The only one proposal that is maintainable, of all this epoch, is the identification of species-group conjugating systematics and homologous chromosomal features [2,14,15]. The fission-fusion theory has been early marginalised by the potentiality of molecular chromosome painting that is now facing a discussion in consideration of the rate of homoplasy that characterizes chromosomal dynamics [16]. Nevertheless, recent cytogenetic results deny a separation of the tribe in two subgroups [17]. Actually the shortage of representative samples, united to the discussed prejudicial position, makes the scarce attempts insufficient for a new interpretation of the phylogeny of the group.

New systematic works supported by a reappraisal in biogeography studies together with DNA level molecular studies and BAC's probe mapping could be extremely valuable for a renewed approach to the study of guenon's evolution.

Cercopithecinae are an engaging example of primate radiation, still offering a huge amount of characters to be investigated in order to achieve a good understanding of evolutionary mechanisms. All possible conservation efforts must be produced for the survival of guenons and related genera in African scene.

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